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COMMENTS ON THE CLASSIFICATION OF RODENTS

By Albert E. Wood

Biology Department, Amherst College

There is no order of mammals where there are so many uncertainties in the current classification as there are in the rodents. The rodents have generally been subdivided into three groups, the Sciuromorpha, Myomorpha and Hystricomorpha, although there have been several attempts (notably Miller and Gidley, 1918, and Winge, 1924) to break away from the tripartite division. The morphologic criteria on which these three groups are based permits living rodents to be marshalled into them with greater or lesser success. But the resulting problems remain very prominent, and well-nigh insuperable when the paleontologic history of the order is taken into account. For example, if the Hystricomorpha are a natural group, how can their present distribution (South America, Africa, southern Europe and south Asia, with scattered recent Latin American immigrants to North America) be explained in view of the complete absence of Tertiary hystricomorphs in North America? Moreover, the morphology of the various genera and families of fossil rodents does not permit these forms to fit into a three-fold classification anywhere near as well as do the living members of the order.

As long as we deal only with the living members of the order, the criteria for subordinal classification can be sorted out fairly well. However, studies of fossil rodents have shown that sometimes the structures on which the classification has been based were independently derived by diverse groups. For example, Wood (1937) showed that the sciuromorph type of zygoma and masseter was developed in the Oligocene genus *Titanotheriomys,* a form that by no stretch of the imagination could be considered to be ancestral to anything included among the recent sciuromorphs.

As a result of general dissatisfaction with the three-fold classification, there have been a number of attempts to arrive at alternative arrangements. Those of Miller and Gidley (1918) and Winge (1924) developed so many additional problems, while solving a few, that they are not generally followed at present.

Wood (1937) basically followed the three-fold arrangement, but proposed a fourth subdivision, the Protrogomorpha, to include the primitive rodents that have not acquired the features of the jaw muscles that characterize the members of the three classic suborders. All members of this suborder are extinct except for *Aplodontia,* the ''Mountain Beaver'' of parts of California, Oregon, Washington and British Columbia.

Simpson (1945) made a valiant attempt to squeeze all rodents into the three-fold classification, though pointing out in many places that the scheme does not work well.

In an extensive review of the early Tertiary rodents of North America, Wilson (1949) followed Simpson's classification but raised many queries and made a number of very significant suggestions, particularly as to the probability of a close relationship between the heteromyids and cricetids, heretofore generally considered to be sciuromorphs and myomorphs, respectively.

Simpson (1950) and Wood (1950) suggested that the South American ''hystricomorphs'' should perhaps be separated as a distinct suborder, though without working out the details. Wood (1955), and Wood and Patterson (in press) are formally carrying out such a separation, with detailed discussion as to the reasons for the change.

Lavocat (1951), in a review of certain Oligocene faunas of France, agreed with this point of view, and showed that the European Eocene and Oligocene Theridomyidae and Pseudosciuridae could not be ancestral to either the Old World or New World hystricomorphs of the present day.

For many years, Stehlin worked on a monograph of the evolution of rodent dentition, which was finished after his death by Schaub (Stehlin and Schaub, 1951). This deals exclusively with the dentition, and develops the thesis that rodents with five-crested teeth are all descended from animals with the basic tooth pattern represented by the European Eocene-Oligocene theridomyids. Although this monograph contains a brief taxonomic section, there is no attempt to present a comprehensive revision of the classification of the order. There are, however, a large number of suggestions and comments which, while not building up any particular classification, must nevertheless be given serious consideration by anyone interested in the supergeneric arrangement of the rodents. I cannot agree with all of Schaub's conclusions, and am therefore attempting to explain some of these differences in detail here. The taxonomic results of these differences of opinion are being published elsewhere as a suggested classification of the rodents (Wood, 1955).

Schaub has recently (1953a) published a revised classification of the ''Hystricomorph'' rodents. In this paper and others (1951, 1953b; Stehlin and Schaub, 1951), he also makes comments on the ''Sciuromorpha'' and ''Myomorpha''. Basically, his idea is that these last two groups are wastebaskets, made up of superfamilies that have had an entirely independent history, and which cannot profitably be grouped in suborders. Although he is not explicit, he gives the impression that he feels that, in one or two cases, there might be some profit in grouping two of the superfamilies into a suborder. With this part of his thesis I feel a great deal of sympathy if not complete agreement, although the classification proposed in Wood, 1955, does not completely follow Schaub in doing away with these suborders. The rodents representing the initial North American Eocene radiation (the Ischyromyoidea), the middle Tertiary to Recent Aplodontoidea, and the Sciuridae certainly seem fairly closely related. At least they all retain primitive features of teeth, of the zygomasseteric region, or of both, and they may well be kept in a common suborder, for which the name Sciuromorpha may be retained. The other superfamilies usually called sciuromorphs seem to be quite distinct from these forms, and may belong in rather diverse parts of the order.

The families that Wood places in the Myomorpha, however, are a group about whose relationships there is little or no certainty. There are some suggestions of mutual relationship, and some indications that Schaub is correct in thinking that they have nothing in common with each other. If they are not related, this would be the end of the Myomorpha, and the superfamilies would have to be either left out of all suborders or, since this is illegal in formal taxonomy, each placed in its own suborder.

It is therefore obvious that Schaub is correct in his contention that the classical concepts of the Sciuromorpha and Myomorpha will have to be abandoned, and either new and perhaps more restricted definitions developed for these suborders, or the subordinal concept will have to be largely abandoned for this order. It is still too early to reach a definite choice between these alternatives.

But on one of Schaub's major points I find myself in disagreement. One of the basic tenets of Stehlin and Schaub's invaluable monograph is that the Theridomyidae are ancestral to all forms that have a five-crested tooth pattern or that are derived from a five-crested ancestor. Schaub has therefore proposed a suborder, Pentalophodonta, to include all forms with five-crested teeth, or that are derivable from a five-crested ancestry. However, it seems no more reasonable to assume that a given tooth pattern has not arisen independently several times than to assume that a given zygomasseteric pattern has not so arisen. Indeed, all the current indications from the study of rodent evolution are that extensive parallelism is the rule rather than the exception in this order. Of Schaub's Pentalophodonta, the South American forms are surely a natural group, the Suborder Caviomorpha of Wood (1955), and the Infraorder Nototrogomorpha of Schaub (1953a). But these forms must have been derived from rodents that entered South America from North America, as is now generally agreed (Schaub, 1953a; Simpson, 1950; Wood, 1950). There is also agreement that this entry must have been no later than late Eocene. Schaub (1953a, p. 393) argues that this ancestral stock could have been theridomyids that crossed North America to reach South America in the Eocene, Paleocene, or even earlier.

It is impossible to prove that a form did not live in an area or at a time where it is not represented by fossils. But no rodents of any kind are known from South America before the Lower Oligocene Deseadan, at which time they have become quite abundant and are beginning to be diversified, although clearly stemming from a common origin. Because of the rapid diversification of the caviomorph rodents beginning with the Deseadan, it seems almost certain that, in this deposit, we are observing an explosive radiation in the process of exploding. A backward extrapolation of the post-Deseadan rate of evolution would indicate that this explosion must have begun not very long prior to the deposition of the Deseado beds. Although such an extrapolation is dangerous, and although we obviously cannot be certain of the reasons for such an evolutionary explosion, by far the most reasonable interpretation, in view of what is known of the general Tertiary history of South America, is that the explosion began with the arrival of rodents in South America. Here was a virgin field, with no highly developed competition, and, once the rodents were established, they rapidly took over all gnawing niches. If this explanation is not correct, it is exceedingly difficult to understand the rapid post-Deseadan development of the caviomorphs. Hence it seems very questionable that rodents could have been present in South America for any appreciable time before the Deseado. If this postulate is accepted, and if their North American origin be granted, most authors consider it more probable that the caviomorphs were derived from known North American types (such as the Paramyidae or Sciuravidae) than from the European Theridomyidae, still unreported from any of the richly fossiliferous North American deposits.

An additional objection to Schaub's suggestion of a Paleocene or even earlier passage of the theridomyids to South America is the complete absence of any rodents from the record prior to the latest Paleocene, when only the single genus *Paramys* is known. Presumably there must have been rodents prior to their earliest appearance in the record, and they may have been in existence for some time, although there is no valid criterion for fixing the length of time necessary to differentiate the rodents from their ancestors. This time may therefore be fixed as long (extending back into the Cretaceous) or short (reaching only the Middle Paleocene), depending on the individual student's opinion as to the probable rates of evolution involved and the significance of the morphologic differences between *Paramys* and whatever group is postulated as the ancestor. Moreover, all the earliest rodents, both in North America and in Europe, are referable to the Paramyidae, and to the most primitive stages of that family. The only non-paramyid lowermost Eocene genus known is the pseudosciurid *Adelomys,* which Wood, in his monograph of the Paramyidae, will indicate was derived from the paramyids.

The absence of theridomyids from North America is, of course, negative evidence. It is possible that this family may have lived in eastern North America where there are no continental Eocene deposits. But there is no evidence that the family was so represented, and it seems highly probable that the rodents that reached South America went by way of what is now Mexico and Central America, and hence were probably derived from the western part of the continent.

Therefore, while admitting that all this is negative evidence, it seems most probable that a representative of one of the known North American Eocene groups reached South America late in the Eocene, to give rise to the South American radiation.

A further point of disagreement with Schaub is in the phylogenetic position of the Paramyidae. Wood (1946) referred to the specialization of the Paramyidae, which indicated that they could not have the fundamental ancestral position generally given them. With this point of view, Schaub is in complete agreement (1953b, p. 35), considering that the Sciuridae have the most primitive tooth pattern in the order. Wood's 1946 opinion was based on preliminary investigation of the paramyids, which includes many rather specialized genera. Further study of Lower Eocene forms, however, has caused a revision of this opinion, and I now feel that the Upper Paleocene and Lower Eocene paramyids are the most primitive known rodents, although it is certain that the earliest sciurids have made little or no advance over them in the structure of the cheekteeth. The data for this conclusion have not been published, but are included in a monograph on the Paramyidae, now nearing completion. Therefore, the North American Paramyidae could have been ancestral to the South American radiation, although the intermediate steps have not been traced in detail. If the paramyids were the ancestors, Schaub's Suborder Pentalophodonta immediately becomes a composite group, the two infraorders having nothing in common.

Schaub places the Theridomyoidea, Castoroidea and Hystricoidea in the Infraorder Palaeotrogomorpha. But Lavocat (1951) has presented evidence, derived from structures other than the cheekteeth, that the theridomyoids cannot be related to the hystricoids, so that this infraorder would also seem to be composite. Schaub places a number of other groups in the Palaeotrogomorpha, particularly the Spalacidae and Rhizomyidae. This seems perhaps somewhat less likely than that they belong in the Myomorpha, if there is any such group. Certainly there is not enough known of the history of either family to justify placing them with confidence in any particular category.

Schaub's new proposals for classification of rodents are very useful and thought-provoking. The fact that there are disagreements with them is not surprising. The current status of rodent phylogeny and classification is such that anyone can point out inconsistencies in anybody else's classification. The rodents are a sufficiently large and complex group so that no one person can be familiar with the entire order. Progress will be made only if various students attack the problem, even though it will result in presenting solutions that others can show obviously to be incorrect. Wood's current (1955) classification has been proposed with this object in view, in the hope that there will be as many criticisms, both constructive and destructive, as possible, since this is the only way to progress.

Schaub has made one further suggestion that very probably will be incorporated in the ultimate classification of the order. This is the idea that many of the superfamilies are entirely separate from all others, presumably having an independent history since the Eocene. There very clearly was a sudden diversification of the rodents, at or near the end of the Eocene, which apparently resulted from a rather sudden change from gnawing based on the use of the temporal muscle to that based largely on the use of the masseter, with consequent enlargement and modification of the latter. The present evidence suggests, but does not prove, that this occurred a great many times independently. It is very probable that these lines all developed from different groups of Eocene rodents, and that, therefore, each of these lines will deserve separate taxonomic treatment. Generally speaking, such superfamilial lines could be grouped into suborders only artificially. Although the present evidence suggests the probability of such a bushy phylogeny (rather than a tree with half a dozen main branches), it is perhaps more conservative to struggle with an attempt to group rodents into suborders for a while longer, while keeping in mind the possibility (or probability) that a classification with entirely independent superfamilies will ultimately prove to be the only one that will fit in with the facts of rodent paleontology, as these gradually come to light. Certainly it will be some time before an adequate classification of the order is compiled.

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